

RESEARCH ARTICLE

Sex-specific trade-offs and compensatory mechanisms: bite force and sprint speed pose conflicting demands on the design of geckos (*Hemidactylus frenatus*)

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SUMMARY

One of the more intuitive viability costs that can result from the possession of exaggerated sexually selected traits is increased predation pressure as a result of reduced locomotor capacity. Despite mixed empirical support for such locomotor costs, recent studies suggest that such costs may be masked by compensatory traits that effectively offset any detrimental effects. In this study, we provide a comprehensive assessment of the locomotor costs associated with improved male–male competitive ability by simultaneously testing for locomotor trade-offs and potential compensatory mechanisms in territorial male and non-territorial female geckos. Fighting capacity and escape performance of male Asian house geckos (*Hemidactylus frenatus*) are likely to pose conflicting demands on the optimum phenotype for each task. Highly territorial and aggressive males may require greater investment in head size/strength but such an enhancement may affect overall escape performance. Among male geckos, we found that greater biting capacity because of larger head size was associated with reduced sprint performance; this trade-off was further exacerbated when sprinting on an incline. Females, however, showed no evidence of this trade-off on either flat or inclined surfaces. The sex specificity of this trade-off suggests that the sexes differ in their optimal strategies for dealing with the conflicting requirements of bite force and sprint speed. Unlike males, female *H. frenatus* had a positive association between hind-limb length and head size, suggesting that they have utilised a compensatory mechanism to alleviate the possible locomotor costs of larger head sizes. It appears that there is greater selection on traits that improve fighting ability (bite force) for males, but it is viability traits (sprint speed) that appear to be of greater importance for females. Our results emphasise that only by examining both functional trade-offs and potential compensatory mechanisms is it possible to discover the varied mechanisms affecting the morphological design of a species.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/216/20/3781/DC1>

Key words: bite force, compensation, *Hemidactylus frenatus*, performance, sprint speed, trade-off.

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INTRODUCTION

Sexual selection is considered the dominant mechanism by which exaggerated sexual traits exhibited by males of many species are shaped (Andersson, M., 1994; Berglund et al., 1996). The evolution of these traits is driven by a trade-off between the benefits accrued to reproduction and the costs incurred because of decreased viability. Reproductive success can be enhanced by the benefits conferred to a male's competitive advantage over other males and increased attractiveness to females (Andersson, S., 1994). The viability costs of exaggerated traits are expected to occur *via* increases in development and maintenance costs and/or compromised survival (Møller and Hedenstrom, 1999; Lopez and Martin, 2002; Oufiero and Garland, 2007; Husak et al., 2011; Husak and Swallow, 2011). One of the more intuitive viability costs for bearing enlarged sexually selected traits is increased predation pressure due to either greater conspicuousness or decreased locomotor performance (Lailvaux and Irschick, 2006; Oufiero and Garland, 2007; Husak and Swallow, 2011). This is because sexual selection may exaggerate such traits beyond the optimum phenotype with respect to biomechanical and/or physiological function, therefore imposing a cost of reduced locomotor performance (Oufiero and Garland, 2007). Despite the logic underlying this mechanism, surprisingly few studies provide compelling evidence that the morphological traits that enhance

reproductive success actually lead to quantifiable decreases in locomotor function (Oufiero and Garland, 2007). For example, the exaggerated fin ornaments of male fish are associated with both poorer swimming performance for some species and improved swimming for others (Ryan, 1988; Basolo and Alcaraz, 2003; Royle et al., 2006; Wilson et al., 2010; Trappett et al., 2013). Furthermore, male sword length was actually positively associated with burst swimming performance for *Xiphophorus nigrensis* (Ryan, 1988), but did not affect swimming endurance for *X. helleri* (Royle et al., 2006).

The lack of convincing empirical evidence for the locomotor costs of exaggerated male traits may be due in part to other unmeasured traits that effectively compensate for the negative impacts on locomotor function and mask their detection (Møller, 1996; Oufiero and Garland, 2007; Husak and Swallow, 2011). Central to this idea is that selection rarely acts on a bivariate relationship between a sexually selected trait and performance in isolation (Lande, 1980; Arnold, 1983; Irschick and Le Galliard, 2008), but rather on the complex interactions among traits (Vanhooydonck et al., 2001; Van Damme et al., 2002; Calsbeek, 2008; Calsbeek and Irschick, 2007). Therefore, natural selection may cause modifications of other traits to counteract the negative effects of sexually selected traits, or 'compensatory traits' (Kirkpatrick, 1987; Møller, 1996; Oufiero and Garland, 2007; Husak and Swallow, 2011). Support for such

Table 1. Summary of details for each of the three test groups: total number of males and females (N), measurements obtained and how these related to the associated aims within the study

Test group	N		Morphology	Bite force	Sprint speed	Aim
	Male	Female				
1	50	50	Yes	Yes	Yes	Relationship between bite force and sprint speed in males and females
			Yes	Yes	Yes	Determinants of dominance
2	50	50	Yes	Yes	Yes	Influence of incline angle on sprint speed
3	50	0	Yes	Yes	Yes	Determinants of prey-capture performance

For final numbers of geckos used in analyses, refer to specific sections within the Materials and methods.

compensatory traits derives from several studies examining the relationship between male ornaments, locomotor function and morphological variation in both birds and insects (Moller, 1996; Husak and Swallow, 2011). For example, Husak et al. (Husak et al., 2011) found that for those species of stalk-eyed flies in which the males possessed wider eye-spans than females, the males also possessed greater relative wing areas. The presumed benefit for possessing greater wing areas, and thus the compensatory mechanism, is the ability to maintain good flight performance despite the potential negative impacts of exaggerated eye-stalks (Husak et al., 2011). However, it is unclear whether such compensatory mechanisms are widespread among other organisms that possess exaggerated sexually selected structures, or whether such mechanisms only act on traits selected for by females rather than via male–male fighting ability (Lailvaux and Irschick, 2006).

Many lizard species engage in male–male combat for access to resources or mates; typically, fights are based on gaping-mouth displays, chasing and biting. In these animals, sexual selection on the underlying functional trait (bite force) could indirectly cause selection for larger head sizes, compromising locomotor function (Anderson and Vitt, 1990; Lopez and Martin, 2002; Huyghe et al., 2005; Husak et al., 2006a; Vanhooydonck et al., 2010). For example, fighting capacity and escape performance are likely to rely upon different suites of morphological traits, potentially placing conflicting demands on an individual’s phenotypic design, which may lead to evolutionary or functional trade-offs (Lewontin, 1978; Garland and Carter, 1994; Vanhooydonck and Van Damme, 2001). Highly territorial lizard species may provide a good model of this functional trade-off, as intrasexual competition may require a greater investment in bite-force performance and thus head size, which may in turn affect overall manoeuvrability and speed of an individual (Lopez and Martin, 2002). Thus, the conflicting demands on an individual’s phenotypic design can result in a compromised phenotype where one motor task is afforded higher performance at the expense of another, or may be compensated by mechanisms that counteract any reduced performance.

In this study, we examined potential trade-offs between those performance functions important to fighting ability (e.g. bite force) and locomotor performance in Asian house geckos (*Hemidactylus frenatus* Schlegel 1836), and tested whether compensatory mechanisms may obscure the detection of such potential locomotor costs. *Hemidactylus frenatus* is an urban-generalist inhabiting most tropical regions worldwide and is rarely seen on the ground, preferring vertical walls and roofs (Hoskin, 2011). Importantly, this gecko is also highly territorial, and males engage in intense agonistic behaviours that frequently escalate into physical combat, including biting (Petren et al., 1993; Hoskin, 2011). Larger relative head sizes would likely enhance fighting ability, but may inhibit locomotor performance, especially on vertical surfaces, because of increased energy expenditure against gravity and associated changes in centre

of mass away from the vertical substrate (Huey and Hertz, 1982; Vanhooydonck and Van Damme, 1999). Geckos use short bursts of speed to capture prey, escape predators and during territorial male–male conflicts (Hoskin, 2011). Therefore, bite force and sprint speed are both ecologically important activities in this species that may act in opposition. We predicted that, because of their combative nature, male geckos would have larger relative head sizes than females, and this would lead to reductions in locomotor performance. In addition, we expected this trade-off to be further exacerbated when individuals sprint on inclined surfaces because of the greater difficulties of running with a large head up inclines as a result of an overall increase in body mass (Huey and Hertz, 1982). Alternatively, if we detected no trade-offs between head size and locomotor performance, then we expected to observe compensatory modifications in relative limb lengths that offset any decrements in locomotor function caused by larger heads.

MATERIALS AND METHODS

Adult male (N=150) and female (N=100) *H. frenatus* were captured from Brisbane, Australia; all geckos had a snout–vent length (SVL) >42 mm and mass >2 g. Three test groups were captured over a 1-year period and maintained in the laboratory for no longer than 3 months. The total number of geckos and specific test groups used in each experiment and final analysis are provided within the relevant sections below (also see Table 1). In the laboratory, geckos were individually housed in well-ventilated plastic terrariums (26×17×13 cm) with a newspaper substrate and a 10×5 cm piece of perforated black plastic piping for a retreat. Terrariums were kept in a temperature-controlled room at 24±1.0°C under a light cycle of 12 h:12 h light:dark. Heat cord (9 m, 90 W) was supplied beneath each terrarium directly below the retreat and was switched on between the hours of 08:00 and 16:00 h, which allowed individuals to self-regulate body temperature. All geckos were fed a diet of calcium-dusted wood cockroaches and crickets every 3 days, and water was misted daily. Individuals that had suffered a loss of more than 10% in body mass, autotomised their tail or suffered other significant health problems during the test period were removed from statistical analyses.

All experiments were approved under the University of Queensland’s Animal Ethics Committee (AEC approval number SBS/319/09).

Relationship between bite force and sprint speed in males and females

We recorded the morphometrics, maximum sprint speed and bite force of 46 male and 49 female *H. frenatus* (Test Group 1). The body mass of each gecko was measured using an electronic balance (±0.01 g; Sartorius Excellence, Göttingen, Germany) at both the start and end of the testing period, with the average of these two measurements used as their measure of body mass. Digital photographs (Casio, EX-

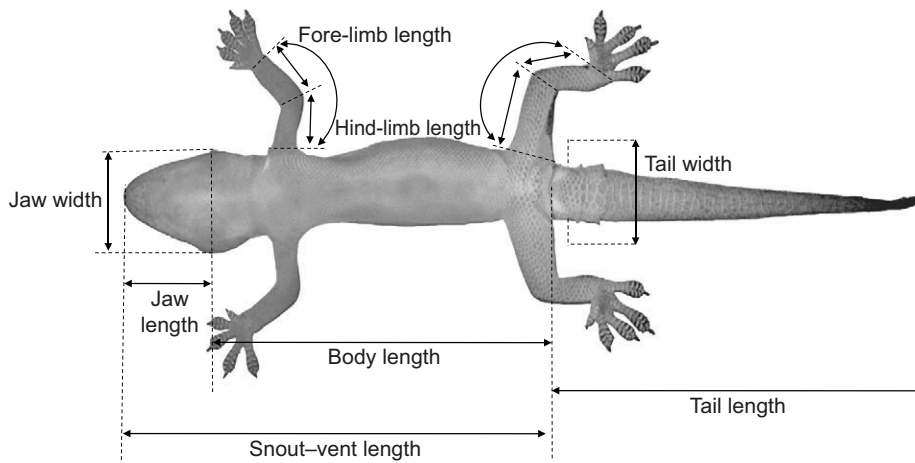


Fig. 1. Photograph of the ventral surface of a male gecko Asian house gecko (*Hemidactylus frenatus*). Morphological variables measured: jaw width (at the maximum lateral extent of the temporal jaw-adductor musculature), jaw length (from coronoid-articular jaw joint to tip of snout), body length (from coronoid-articular jaw joint to cloaca) average fore-limb length (humerus and radius), average hind-limb length (femur and fibula), tail width (pre-caudal autonomy vertebrae) and tail length (cloaca opening to tip of tail). Snout-vent length (SVL; sum of jaw length and body length) is also shown as it was used in various analyses. All variables were combined for each individual via principal component analyses to gain an overall measure of body size (PC_{Body} ; seven variables, excluding SVL) and head size (PC_{Head} ; jaw width and jaw length).

FH25, China) of the ventral surface of individual geckos were taken to measure seven different body dimensions (Fig. 1): jaw width (at the maximum lateral extent of the temporal jaw-adductor musculature), jaw length (coronoid-articular jaw joint to tip of snout), body length (coronoid-articular jaw joint to cloaca), average fore-limb length (humerus and radius), average hind-limb length (femur and fibula), tail width (pre-caudal autonomy vertebrae) and tail length (cloaca to tip of tail). All digital photographs of individuals were taken at the end of the test period. As all experiments were less than 2 months in duration and body mass did not vary by more than 10% for each individual across this period, growth was minimal during the experiments. Images were calibrated and analysed using morphometric software (SigmaScan 5.0, Systat Software, San Jose, CA, USA). Principal component analyses (PCAs) were used to combine seven morphological variables (SVL was excluded) into an overall measure of body size (PC_{Body}), and jaw width and jaw length were used as measures of head size (PC_{Head}). All PCA measures were calculated with the sexes combined. Overall body size of *H. frenatus* is represented by PC_{Body} (first principal component), which accounted for 57% of the variation in the data (Table 2). All loadings were positive, indicating that all seven morphological variables increased together. This species exhibits caudal autotomy; therefore, tail length is not as influential as all other morphological variables (only 0.108 variation explained; see Table 2) in PC_{Body} . All geckos that autotomised their tails during testing were excluded from analyses. We also calculated a measure of condition for each individual by calculating residuals of a linear regression of log-transformed body mass by log-transformed SVL.

Maximum bite force was measured using a custom-built sensor consisting of two metal plates ($8 \times 25 \times 1$ mm) separated by a larger third steel metal pivot plate (3 mm thick), with all three plates permanently secured to form one unit. The two smaller plates protruded 12 mm beyond the pivot plate. The top metal plate had a strain gauge (RS Electronics, Sydney, Australia) attached via epoxy resin. The output from the strain gauge was connected to a custom-made Wheatstone bridge linked to a bridge amplifier (ADInstruments, Sydney, Australia) (Wilson et al., 2007). The two protruding plates were covered in three layers of flesh-like tape (Elastoplast, Beiersdorf, North Ryde, NSW, Australia) to offer a defined biting point and surface. Output from the bridge amplifier was monitored via a data recording system (PowerLab, ADInstruments). A series of weights ranging from 100 to 1000 g were suspended from the bite point to calibrate the output. Calibrations reflected the force applied during bites to the biting

point. The strain gauge was calibrated daily prior to use so that the voltage output from the bridge amplifier could be converted to force (N).

Geckos were briefly induced to bite forcefully on the 'bite point' of the sensor by placing the bite plates between the gecko's open jaws. If a maximum bite was not attained or biting did not occur on the 'bite point', geckos were rested and a second attempt was made after 10 min. A minimum of five maximum bites per individual were recorded in each of the two separate test periods, with 2 weeks between each test period (repeatability of maximum bite forces was calculated using the single best performance for each individual from each test period; Pearson's product-moment correlation, $r=0.81$, d.f.=200, $P<0.001$). The maximum of the 10 bites was used as the measure of an individual's bite force (N). Prior to measuring maximum bite force, all geckos were equilibrated to $24 \pm 1^\circ\text{C}$ in a temperature-controlled room for a minimum of 90 min.

Maximal sprint speed was measured using a custom-built Perspex runway ($100 \times 7 \times 10$ cm) fitted with four infrared LED light gates. Light gates were positioned towards the middle of the runway at 10 cm intervals. Output from the LED light gates was monitored via a four-channel data recording system (PowerLab, ADInstruments). Sprints were elicited by placing individuals in the start position of the runway and chasing them to the opposite end using a foam brush the width of the runway. Geckos were made to run along the runway four times during each test period. Sprint speed was then calculated for each of the three 10 cm

Table 2. Summary of the principal component analysis (PCA) for body dimensions of *Hemidactylus frenatus* (PCA includes both sexes from Test Group 1)

Morphological variable	PC_{Body}	PC 2	PC 3	PC 4
Jaw width	0.455	0.234		
Jaw length	0.429	0.133		
Body length	0.453	0.175		-0.317
Tail width	0.395	0.254	0.368	0.521
Tail length	0.108	-0.645	0.722	-0.200
Fore-limb average	0.280	-0.582	-0.422	0.588
Hind-limb average	0.397	-0.279	-0.307	-0.489
Percentage of variance	57%	16%	13%	4%

Values represent the relative contributions of each of the seven morphological variables (see Fig. 1) towards each of the components. Missing values indicate loadings less than 0.1. PC_{Body} explains 57% of the variation and corresponds to overall body size with all variables loading positively.

distances between consecutive light gates for all four runs during each testing period (i.e. 12 measures of sprint speed per testing period) (Hertz et al., 1982; Angilletta et al., 2002; Adolph and Pickering, 2008). All geckos were then re-tested in the same manner after a 2 week rest period (repeatability of maximum sprint speeds was calculated using the single best performance for each individual from the two test periods; Pearson's product-moment correlation, $r=0.13$, d.f.=300, $P=0.023$). From the 24 time splits recorded per individual, the fastest was then used as their measure of maximum sprint speed (cm s^{-1}). Prior to measuring maximum sprint speed, all geckos were equilibrated to $24\pm 1^\circ\text{C}$ in a temperature-controlled room for a minimum of 90 min.

Influence of incline angle on sprint speed

We examined the influence of incline angle on the sprint speed of 44 male and 47 female *H. frenatus* (Test Group 2). We quantified sprint performance of each individual at 0 and 60 deg by adjusting the incline angle of the custom-built runway. Individual bite force and morphology was also quantified. These two angles were chosen, excluding a 90 deg angle, as geckos would not sprint consistently on a vertical incline on the Perspex substrate. A 60 deg incline was the maximum angle on which sprint speed remained significantly repeatable. Sprint speed was measured using methods identical to those outlined above and the order for testing performance at each incline angle was randomised for each individual. The proportional decrease in sprint speed was calculated by sprint speed at 60 deg divided by sprint speed at 0 deg (60 deg/0 deg). The morphology of each individual gecko and bite force were also quantified (as above) to determine the influence of overall head size and biting capacity on the relative decrease in sprint speed with an increase in incline.

Determinants of dominance

We recorded the morphometrics, bite performance, sprint speed and dominance of individual male geckos (from Test Group 1) in staged dyadic bouts (25 focal males and 25 male opponents). Opponents were divided into three size classes (small, medium and large) by body mass. Each focal male was competed against a randomly selected opponent male, one from each of the size classes in random order. Size classes were used as we were interested in all factors, and interactions, that affect the outcome of male fights, and it is also well documented that body size can affect dominance (Perry et al., 2004). All males (focal and opponent) were competed a total of three times, with individuals never encountering the same male twice. All 75 bouts were conducted within a darkened, temperature-controlled room set at $24\pm 1^\circ\text{C}$. Geckos were equilibrated to 24°C for 90 min whilst maintained in their individual terrariums before each bout and received a 48 h rest period between bouts.

To start each bout, focal and opponent geckos were simultaneously introduced to opposite sides of a $60\times 30\times 30\text{ cm}$ sealed glass terrarium. A limited resource (heat point in the tank) was provided to facilitate interactions between males. Each focal gecko was marked with three small dots of neutral white non-toxic acrylic paint for identification – on the dorsal side of the head and torso and the tip of the tail (Lailvaux et al., 2004; Jenssen et al., 2005). To allow all observations to be conducted in darkness, thus excluding observer effects and representing nocturnal activity, each bout was filmed using a Sony handheld camera (Sony DCR-HC52E, Tokyo, Japan) on night-shot setting using infrared lights. Each bout was recorded for 30 min from the time of initial introduction to the arena. This period allowed sufficient time for one of the individuals to attain dominance, as geckos generally interacted immediately.

We scored each male's dominance status using a range of observed behaviours, with the scoring system modified from studies of dominance in other lizard species (Garland et al., 1990; Lailvaux et al., 2004; Perry et al., 2004; Huyghe et al., 2005; Lailvaux and Irschick, 2007). As the dominance behaviour of *H. frenatus* has not previously been studied, we used pilot studies to rate each interactive behaviour, with more frequent and less aggressive or submissive behaviours receiving lower scores in comparison to less frequent, more costly and territorial behaviours. Both focal and opponent males were scored on a scale that reflected their aggressiveness (i.e. bite, 3 points; nudge, 2 points; body arch, 2 points; chase, 2 points; tail wag, 1 point; and access to limited resource, 0.5 points). Submissive behaviours received negative points depending on the level of subordination (i.e. retreat/avoidance, -3 points; and chased away, -2 points). Extra points were awarded or deducted for winning or losing a direct physical fight (1 and -1 points, respectively), with no result yielding zero points. Dominance rankings were based on an individual focal male's overall score across all three bouts (focal male score minus that of their opponents). Male geckos that lost more than 10% of body mass and/or autotomised their tale, at any point during the test period, were excluded from analyses (focal $N=2$, opponent $N=2$).

Determinants of prey-capture performance

We recorded the morphometrics, bite performance, sprint speed and prey capture performance of 50 individual male geckos (Test Group 3). To quantify prey capture ability, we assessed each individual's capacity (total time taken in seconds; where 0 s is the fastest prey capturing ability and 600 s is the slowest) to capture live crickets (*Acheta domesticus*) during staged feeding trials (modified from Verwajen et al., 2002). All feeding trials were conducted within a temperature-controlled room set at $24\pm 1^\circ\text{C}$ and within the geckos' permanent terrarium so as to reduce stress. Each gecko was fasted for 3 days prior to testing and all substrate, excess food and waste was removed from the terrarium. To exclude observer effects, each trial was filmed using a Sony handheld camera and recorded for 10 min from the time of the initial introduction of the prey ($130\pm 20\text{ mg}$). If a gecko had not captured the prey within this time they received the total time of 10 min (600 s), the cricket was removed and the trial was ended. One prey item was introduced into each terrarium each day for five consecutive days. Maximum prey capture was the fastest time (0–600 s) of the five trials for individual geckos. If the gecko did not capture any prey during these five trials they were removed from the analysis ($N=5$) with the assumption that they were unmotivated or too stressed. Time to capture prey was repeatable with no significant difference between each trial (one-way ANOVA with Tukey's HSD *post hoc* comparison: $F_{4,245}=0.80$, $P=0.53$).

Statistical analysis

Statistical analyses were performed using R (version 2.11.1, R Foundation for Statistical Computing, Vienna, Austria) unless otherwise specified. Significance was taken at the level of $P<0.05$. Both Pearson's product-moment correlations and multiple linear regressions with model simplification were used to establish whether morphology and/or sex affected performance. We calculated size-corrected measures of morphological traits (head size, fore- and hind-limb lengths, tail width and tail length) by generating residual values of the particular trait regressed on SVL.

A multiple linear regression was used to investigate whether there was a functional trade-off between bite force and sprint speed. We examined the relationship between relative head size

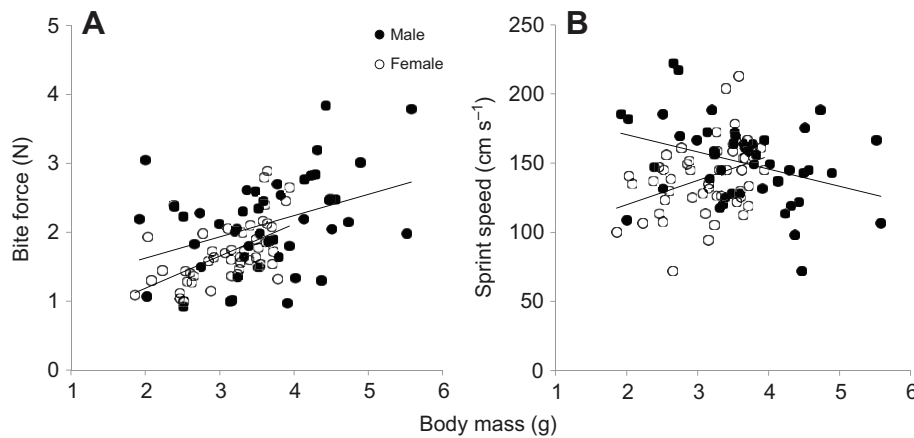


Fig. 2. The relationship between body mass (g) and (A) bite force (N) and (B) sprint speed (cm s^{-1}) in *Hemidactylus frenatus*. Males ($N=47$) are represented by full circles and females ($N=49$) by empty circles. There was a significant positive effect of mass on bite force but not of sex or any interaction between the two predictors ($R^2=0.353$, $F_{1,96}=52.45$, $P<0.001$). Sex, mass and an interaction of predictors had a significant effect on sprint speed ($R^2=0.14$, $F_{3,94}=6.03$, $P<0.001$).

and bite force with the proportional decrease in sprint speed up an incline using Pearson's product-moment correlation for each sex separately. To assess whether compensation was masking any potential trade-offs, we investigated the relationships between relative head size and other morphological variables that could affect sprint speed. Males and females were analysed separately using a Pearson's product-moment correlation. Furthermore, to investigate whether hind limb length is a potential compensatory mechanism, we used residuals of relative head size on relative hind-limb length. This measure of hind-limb length corrected for head size was then used to identify whether compensation resulted in increased locomotor performance (sprint speed), off-setting costs of increased head size *via* a Pearson's product-moment correlation, again with sexes analysed separately.

Path analyses were used to describe the relationship between morphological and performance traits with both dominance and prey-capture abilities (AMOS 5.0, SPSS, Chicago, IL, USA). The model design is modified from Oufiero and Garland (Oufiero and Garland, 2007) to assess body mass (as these would co-vary with sexually selected traits and may influence performance capacity), sexually selected traits, compensatory traits, performance and the effects on fitness [see fig. 1 in Oufiero and Garland (Oufiero and Garland, 2007)]. The morphological measures of body mass (g), condition (as described above), head size (PC_{Head}) and hind-limb length (mm) were used in combination with the two performance traits of bite force (N) and sprint speed (cm s^{-1}). Ten models describing the relationship between these variables with either dominance or prey capture were tested. The most complex model included all interactions (Model A), while simplified versions contained varying combinations of the variables (models B–J; see supplementary material Fig. S1). All 10 models for dominance and prey capture were ranked by calculating the second-order Akaike's information criterion (AIC_c):

$$\text{AIC}_c = \chi^2 + 2K + [2K(K+1)] / (N-K-1), \quad (1)$$

where χ^2 is the chi-square goodness of fit, K is the number of estimated parameters and N is the sample size (Angilletta et al., 2006). AIC_c values were used to assess which model explained the most variation in dominance and prey capture in relation to model complexity by Akaike weights (w_i).

RESULTS

Relationship between bite force and sprint speed in males and females

Male *H. frenatus* were on average 20% larger than females (mean male mass = 3.61 ± 0.10 g, $\text{PC}_{\text{Body}} = 1.08 \pm 0.29$; mean female

mass = 3.01 ± 0.07 g, $\text{PC}_{\text{Body}} = 1.00 \pm 0.18$). Head size (PC_{Head}) scaled positively with overall body size (PC_{Body}) for both sexes ($r=0.94$, d.f.=96, $P<0.001$), with males possessing larger overall head sizes than females (mean male $\text{PC}_{\text{Head}} = 0.61 \pm 0.2$, mean female $\text{PC}_{\text{Head}} = -0.70 \pm 0.13$).

Bite force was significantly positively associated with body size ($R^2=0.353$, $F_{1,96}=52.45$, $P<0.001$; Fig. 2A) and head size ($R^2=0.306$, $F_{1,96}=42.44$, $P<0.001$). In both cases there was no significant effect of sex on bite force (body size: $t=0.467$, $P=0.642$; head size: $t=0.797$, $P=0.428$), nor were there any significant interactions between sex, bite force and size (body size: $t=0.015$, $P=0.988$; head size: $t=-0.107$, $P=0.915$). Overall, males had stronger bite force than females; however, there was no difference once corrected for body size (PC_{Body}) ($R^2=0.006$, $F_{1,96}=0.61$, $P=0.437$). Sprint speed was significantly associated with body mass ($t=2.53$, $P=0.013$) and sex ($t=3.99$, $P<0.001$), though in opposite directions for males and females. Male sprint speed decreased with increasing body mass, whereas female sprint speed increased with increasing body mass ($R^2=0.14$, $F_{3,94}=6.03$, $P<0.001$; Fig. 2B). A similar trend for the effects of body size (PC_{Body}) and sex on sprint speed were observed; however, it was not statistically significant (body size: $t=1.72$, $P=0.097$; sex: $t=1.00$, $P=0.319$; body size \times sex: $t=-1.74$, $P=0.085$).

The relationship between bite force and sprint speed was significantly affected by sex ($R^2=0.106$, $F_{3,94}=3.72$, $P=0.014$), with males displaying a negative relationship between these two traits. Bite force was negatively correlated with sprint speed for male *H. frenatus* ($r=-0.315$, d.f.=46, $P=0.029$; Fig. 3A); however, females showed no significant relationship between bite force and sprint speed ($r=0.194$, d.f.=48, $P=0.178$; Fig. 3B).

Determinants of dominance and prey-capture performance

Among the 10 path models, Model I best described the relationships among morphology, performance and dominance ($\chi^2=26.5$, d.f.=7, $K=20$, $\text{AIC}_c=50.7$, $w_i=0.35$; Fig. 4A, supplementary material Table S1). Within this model, dominance was significantly positively associated with bite force ($P=0.004$), while sprint speed had a negative relationship ($P=0.136$). Hind-limb length had no significant effect on either bite force ($P=0.887$) or sprint speed ($P=0.983$), and was not related to body mass ($P=0.408$). However, head size was significantly positively associated with both body mass ($P<0.001$) and bite force ($P=0.001$). Overall, male body mass and head size affected dominance *via* their influence on bite force but not sprint speed. A similar trend was seen in the second most likely model, Model G ($\chi^2=17.9$, d.f.=6, $K=21$, $\text{AIC}_c=51.2$, $w_i=0.256$), with the addition of a significantly positive covariance between head size and hind-limb length ($P=0.016$).

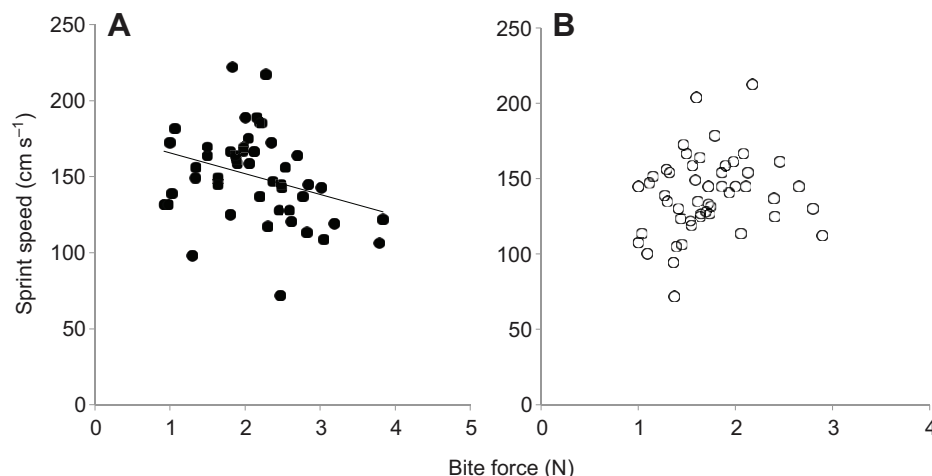


Fig. 3. The relationship between bite force (N) and sprint speed (cm s^{-1}) for (A) male and (B) female *Hemidactylus frenatus*. There was a significant negative correlation (trade-off) between bite force and sprint speed for males ($r = -0.315$, d.f. = 46, $P = 0.029$) but not for females ($r = 0.194$, d.f. = 48, $P = 0.178$).

The relationships among morphology, performance and prey-capture ability were more than 60% likely to be best described by Model G ($\chi^2 = 5.2$, d.f. = 6, $K = 21$, $\text{AIC}_c = 38.6$, $w_i = 0.60$; Fig. 4B, supplementary material Table S2). Based on this model, bite force ($P = 0.002$), but not sprint speed ($P = 0.603$), was negatively correlated with an individual's prey capture time. Thus geckos with stronger bites captured prey faster than those with weaker bites. For prey-capture performance, body mass was significantly positively correlated with head size ($P = 0.002$) as well as hind-limb length ($P = 0.069$); head size and hind-limb length were also positively correlated ($P = 0.004$). In this model, individuals with larger heads also had stronger bites and faster sprint speeds ($P = 0.106$), but hind-limb length was not related to either of the performance traits (bite force: $P = 0.501$; sprint speed: $P = 0.420$).

Influence of incline angle on sprint speed

A gecko's sprint speed at 60 deg incline as a proportion of speed at the horizontal was not affected by body size (PC_{Body}) ($t = -1.806$, $P = 0.074$), but sex did affect this proportion ($t = 2.26$, $P = 0.026$). Larger males had slower sprint speeds at a 60 deg incline as a proportion of their speed at the horizontal ($R^2 = 0.054$, $F_{2,92} = 2.64$, $P = 0.076$). Bite force ($t = -2.01$, $P = 0.047$) and sex ($t = 2.40$, $P = 0.018$) independently affected the proportional decrease in sprint speed, with increases in the bite force of males associated with lower sprint speeds at a 60 deg

incline relative to their speed at the horizontal ($R^2 = 0.062$, $F_{2,92} = 3.04$, $P = 0.050$). As male head size (PC_{Head}) increased, we also observed a decrease in sprint speed between the two inclines ($r = -0.329$, d.f. = 44, $P = 0.026$; Fig. 5A); however, this relationship was absent in females ($r = 0.006$, d.f. = 47, $P = 0.969$; Fig. 5B).

Compensatory traits

We found no significant relationship between relative head size and any of the relative morphological variables for male *H. frenatus* [relative fore-limb length: $r = -0.127$, d.f. = 44, $P = 0.401$; relative hind-limb length (Fig. 6A): $r = 0.091$, d.f. = 44, $P = 0.548$; relative tail width: $r = 0.070$, d.f. = 44, $P = 0.643$; relative tail length: $r = -0.045$, d.f. = 44, $P = 0.758$]. In females, however, relative head size was significantly positively correlated with both relative hind-limb length ($r = 0.307$, d.f. = 47, $P = 0.032$; Fig. 6B) and relative tail width ($r = 0.420$, d.f. = 47, $P = 0.003$); that is, females that had proportionally longer hind limbs and wider tails also had relatively larger heads. In contrast, relative fore-limb length ($r = 0.267$, d.f. = 47, $P = 0.063$) and relative tail length ($r = 0.111$, d.f. = 47, $P = 0.449$) were not significantly associated with relative head size for females. For both sexes, sprint speeds were not affected by relative hind-limb length, corrected for relative head size, at either 0 deg (males: $r = 0.185$, d.f. = 44, $P = 0.218$; females: $r = -0.190$, d.f. = 47, $P = 0.191$) or 60 deg inclines (males: $r = -0.075$, d.f. = 44, $P = 0.621$; females: $r = -0.071$, d.f. = 47, $P = 0.623$).

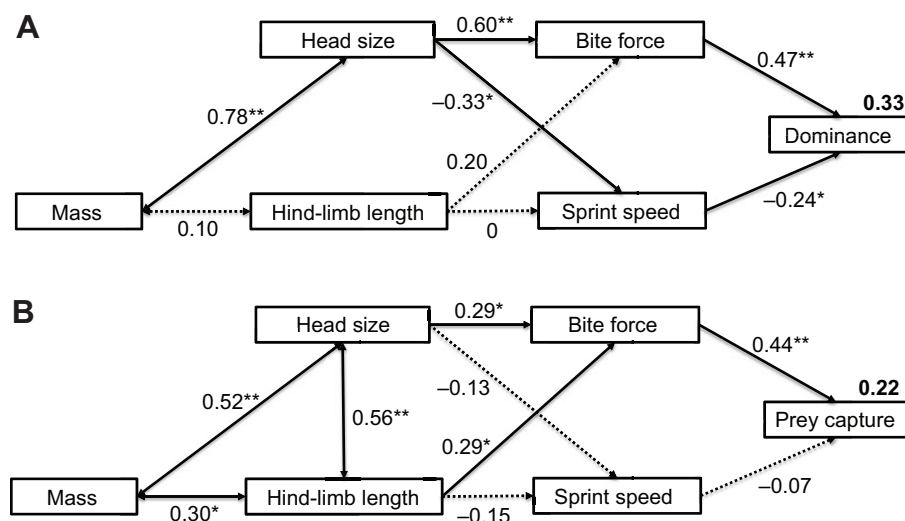


Fig. 4. The best predictive models described by path analyses and selected by AIC_c which describe the relationships among morphological traits [body mass (g), head size and hind-limb length (mm)], performance traits [bite force (N) and sprint speed (cm s^{-1})] and (A) dominance (Model I; see supplementary material Fig. S1I), which explains 33% of the variation in dominance (value in bold), and (B) prey capture (Model G; see supplementary material Fig. S1G), explaining 22% of the variation in time to capture prey for male *Hemidactylus frenatus*. Standardized coefficients are provided for each path (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

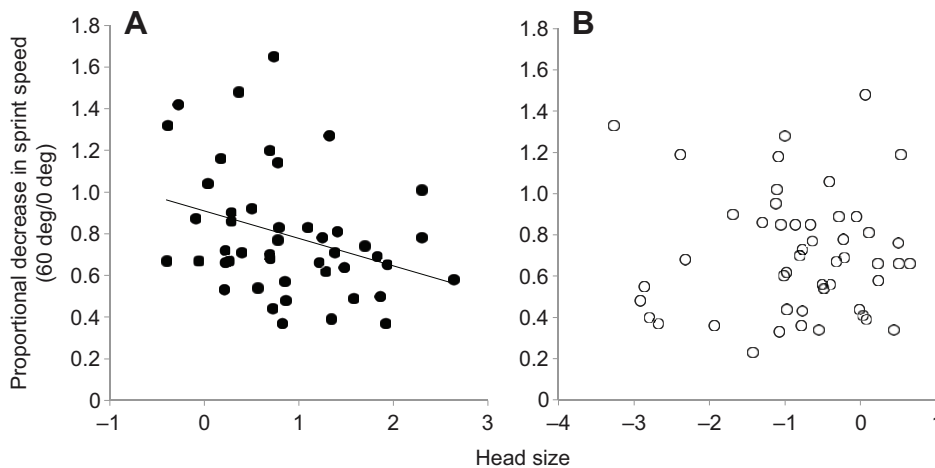


Fig. 5. The relationship between head size (PC_{Head}) and sprint speed of geckos at a 60 deg incline as a proportion of sprint speed at no incline (0 deg) for (A) male and (B) female *Hemidactylus frenatus*. There was a significant negative correlation (trade-off) for males ($r=-0.329$, d.f.=44, $P=0.026$) but no significant correlation for females ($r=0.006$, d.f.=47, $P=0.969$).

DISCUSSION

Selection rarely acts on a single trait in isolation, but rather on a combination of traits (Calsbeek and Irschick, 2007). In our study, we investigated how differing selection pressures on performance traits may result in a compromised phenotype (trade-off); specifically, we evaluated trade-offs between traits linked to dominance (bite force) and prey capture or predator avoidance (sprint speed). We also investigated whether any compensatory mechanisms offset some of the associated reductions in performance. We found support for our prediction that a trade-off exists between those traits associated with bite force and those associated with locomotor performance in the Asian house gecko (*H. frenatus*). Males that had a greater biting capacity because of larger head sizes suffered reduced sprint performances, and this trade-off was further exacerbated when sprinting on an incline. Females, however, showed no evidence of this trade-off on either flat or inclined surfaces. The sex specificity of this trade-off suggests that males and females may differ in their optimal strategies for dealing with the conflicting requirements of bite force and sprint speed. Females with larger heads also had longer hind limbs, indicating the possible presence of a compensatory mechanism to reduce the locomotor costs associated with head size.

The magnitude of sexual dimorphism varies greatly among species and may reflect the divergent selective pressures operating on each sex, and among different species (Herrel et al., 2012). We expected that the high level of territoriality and combat exhibited by male *H. frenatus* would result in larger relative head sizes for males. However, we did not find this to be the case. Males were

larger than females in overall body size but not relative head size. Larger body sizes in the males of other lizard species are associated with increased bite performances and success in territorial combats (e.g. Anderson and Vitt, 1990; Herrel et al., 1996; Herrel et al., 1999; Verwajen et al., 2002; Lailvaux et al., 2004; Huyghe et al., 2005). Our path analyses of dominance hierarchies support this idea, and demonstrate that an increase in body size leads to greater male–male combat success; bite force was the most important performance trait, of the traits measured, underlying male success in territorial combats. Recent studies have found similar correlations between bite force and dominance in other lizard species (Lailvaux et al., 2004; Huyghe et al., 2005). For example, Huyghe et al. (Huyghe et al., 2005) found that in *Gallotia galloti*, bite force was the most important predictor of the outcome for male–male combat. These findings suggest that there may be direct sexual selection for increased bite force in both *H. frenatus* and *G. galloti* males, which provides an advantage during male–male combat and possibly mating with females, indirectly driving the increase in head size or, in this case for *H. frenatus*, overall body size (Lappin et al., 2006; Husak and Swallow, 2011).

The functional trade-off we observed between bite force and sprint speed performance in male *H. frenatus* suggests the presence of conflicting demands on male fighting ability and locomotor performance (Lopez and Martin, 2002); the locomotor performance of dominant, larger-headed males was even poorer on inclines. We believe these results demonstrate how habitat selection can mediate the expression of functional trade-offs: the narrow crevices and compact retreat sites utilised by *H. frenatus* for anti-predatory

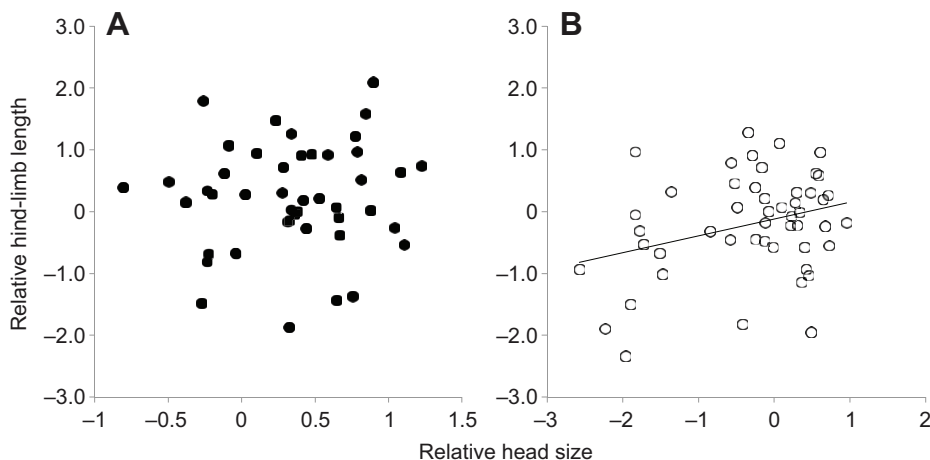


Fig. 6. Relationship between relative head size (residual PC_{Head} by SVL) and relative hind-limb length (residual hind limb by SVL) for (A) male and (B) female *Hemidactylus frenatus*. There was a significant positive correlation for females ($r=0.307$, d.f.=47, $P=0.032$) but not for males ($r=0.091$, d.f.=44, $P=0.548$).

behaviour may explain why males do not exhibit increased relative head sizes compared with females (Lappin et al., 2006; Hoskin, 2011). Other lizard species inhabiting vertical surfaces also tend to have a reduced head to body ratio, which allows the centre of mass to be kept closer to the substrate, reducing the tendency to topple backwards (Vanhooydonck and Van Damme, 1999; Verwaijen et al., 2002). Therefore, to retain the ability for a greater biting capacity, whilst remaining within the constraints of the chosen habitat, males may increase overall body sizes but not relative head sizes. However, the absence of sexual dimorphism in relative head size in *H. frenatus* may also be due to the importance of biting capacity for both males and females (Herrel et al., 1998; Verwaijen et al., 2002; Vincent and Herrel, 2007). Although not investigated in this study, increased bite force and therefore head size in female *H. frenatus* may also be under natural selection to increase prey-capturing ability, resulting in a bigger head, as is the case for male *H. frenatus*. Even though prey capture is likely to be more complex than our model assumes, previous studies also suggest that both bite force and head morphology are highly relevant for feeding capacity and ability to capture food, and are therefore under natural selection (Herrel et al., 1998; Verwaijen et al., 2002; Verwaijen and Van Damme, 2007; Vincent and Herrel, 2007; Kaliontzopoulou et al., 2012).

In contrast with our study, several previous studies have found greater locomotor performance to be positively associated with social dominance (Garland et al., 1990; Hews, 1990; Robson and Miles, 2000; Lailvaux et al., 2004; Perry et al., 2004; Husak et al., 2006b; Peterson and Husak, 2006; Hall et al., 2010). However, a study by Huyghe et al. (Huyghe et al., 2005) found no correlation between locomotor performance and dominance, but rather between increased bite force capacity and dominance (Huyghe et al., 2005). The direct functional importance of locomotor performance to dominance is difficult to determine; it may not be directly related to individual combat success, but rather may be a more general indicator of overall male quality (e.g. Lailvaux et al., 2004; Hall et al., 2010). Lopez and Martin (Lopez and Martin, 2002) found a trade-off between head size and locomotor performance for the lizard *Lacerta monticola*; unlike male *H. frenatus*, however, it appears that this trade-off was attributable to reduced energy allocation during the breeding season and not a biomechanical constraint (Lopez and Martin, 2002). However, bite force of *L. monticola* in this study was not assessed. These contrasting results may be a result of differing social and sexual behaviours and fighting strategy, with selection for different performance variables. However, intraspecific variation in characteristics such as foraging ability, predation intensity and habitat selection and the role they play on how sexually selected traits may evolve could also be of great importance (Petren and Case, 1998; Huyghe et al., 2005).

We found that female *H. frenatus* with relatively larger heads also had relatively longer hind limbs. This morphological correlation was the likely mechanism for the absence of a trade-off between bite force and sprint speed within females. In contrast, male *H. frenatus* showed no such modification in limb length, and males that had larger heads may have suffered reduced locomotor performance as a consequence. However, these assessments are merely speculative; though previous studies report limb length as an important determinant of sprint speed (Vanhooydonck et al., 2001; Husak, 2006), we did not find a correlation between relative hind-limb length (corrected for head size) and sprint speed in geckos. This result, however, may be due to the low repeatability of, or noise within, measures of sprint speed of individuals. Male *H. frenatus*, however, did not provide evidence for a compensatory increase in limb length to mediate any reduction in locomotor

performance. This may be due to males having varying energy allocation requirements to achieve and maintain a certain level of dominance, such as increased body size and production of testosterone (Sinervo et al., 2000; Husak et al., 2007). However, it seems that there are alternate costs for possessing larger heads for male and female *H. frenatus*. Males pay the direct costs on locomotor performance while females pay an energetic cost through investment in longer limbs.

Taken together, our results clearly suggest that performance trade-offs may limit the exaggeration of sexually selected traits, but such costs have the potential to be mitigated by compensatory morphological changes. For *H. frenatus*, this suggests that there is a greater selection on traits associated with dominance (i.e. bite force) for males and survival (i.e. sprint speed) for females.

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AUTHOR CONTRIBUTIONS

S.F.C. and R.S.W. conceived and designed the experiments; S.F.C. and M.L.W. collected the data; S.F.C. analysed the data; and S.F.C. and R.S.W. wrote the paper.

COMPETING INTERESTS

No competing interests declared.

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